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Population status of the Illinois chorus frog
(*Pseudacris streckeri illinoensis*)
in Madison County, Illinois: Results of 1996 surveys

IDOT CONTRACT 1-5-90179

FINAL REPORT ON 1996 RESULTS

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DISCLAIMER

The findings, conclusions, and views expressed herein are those of the researchers and should not be considered as the official position of the Illinois Department of Transportation.

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EXECUTIVE SUMMARY

A study of the biology of the Illinois chorus frog, *Pseudacris streckeri illinoensis*, is reported. Surveys of Madison County for choruses of the frogs located seven choruses in 1996. These choruses were located at the same sites that choruses were found in 1994-1995. No frogs were found at historical sites near Granite City, South Roxana, or New Poag Road similar to results in 1994-1995. The bulk of the study was conducted using drift fences at the recently purchase wetland mitigation area adjacent to Sand Road in Sec. 19, T4N, R8W. The primary purpose of the 1996 study was to estimate population size and density at the mitigation area. We again estimated population size using recaptures of frogs previously marked. We arrived at a density estimate for this species of 0.001 frogs/m^2 using the number of frogs found exiting polygons placed at the site. Assuming that about 7.1 h of suitable sand habitat existed at the mitigation area, then the density estimate of 0.001 *Pseudacris streckeri illinoensis*/m^2 would suggest that 71 frogs should be expected to occupy this area. In contrast, Lincoln-Petersen index estimates of population size based on recaptures of previously marked frogs were 99 ± 18.9 frogs for females and 80 ± 16.2 frogs for males based on 3 recaptures of 18 marked females and 5 recaptures of 20 marked males. Thus, a rough population estimate overall would be about 179 individual adult *P. s. illinoensis*. The difference between population estimates based on density estimates vs. those based on mark-recapture estimates may reflect errors inherent in estimating population size in a rare fossorial anuran. However, some of the difference likely reflects the influx of *P. streckeri* from neighboring areas onto the mitigation area to take advantage of suitable chorus sites located on the mitigation area. We found that this species was not freeze tolerant. Thus manipulations of the site need to be carefully considered to avoid increasing the depth to which the soil freezes. Frogs exposed to freezing temperatures will die. Our prelimanary analysis suggests that reduction in vegetative cover will no increase risk of overwinter mortality.

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ACKNOWLEDGMENTS

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INTRODUCTION

The Illinois chorus frog, *Pseudacris streckeri illinoensis*, is restricted to areas of sandy substrates found in the floodplains of the Mississippi and Illinois rivers in Arkansas, Illinois, and Missouri (Conant and Collins, 1991). Because these habitats have been converted to agriculture or developed for other human activities, *P. s. illinoensis* is now uncommon. It is listed as a threatened species in Illinois (Herkert, 1992), as a rare species in Missouri (Anonymous, 1992), as a species of special concern in Arkansas (R. Roberg, pers. comm.), and as federal C-2 species (Dodd et al., 1985).

This highly fossorial frog is distributed in Illinois mainly along the central part of the Illinois River (Smith, 1951, 1961, 1966; Morris and Smith, 1981; Taubert et al., 1982; Brown and Rose, 1988; Morris, 1990; Beltz, 1991 and 1993). Other populations are, also, scattered along the Mississippi River floodplain from Madison to Alexander Counties, Illinois (Holman et al., 1964; Brown and Brown, 1973; Axtell and Haskell, 1977; Morris and Smith, 1981; Taubert et al., 1982; Gilbert, 1986; Brown and Rose, 1988; Morris, 1990; Beltz, 1991 and 1993; Tucker and Philipp, 1993; 1994; 1995).

Several previous publications and unpublished reports provide details on the life history of *P. s. illinoensis* including information on underground feeding behavior (Brown, 1978), burrowing behavior (Axtell and Haskell, 1977; Brown et al., 1972; Tucker et al., 1995; Tucker, 1995), chorus sites (Brown and Rose, 1988), fecundity (Butterfield et al., 1989; Tucker and Phillip, 1995; Tucker, 1997a), post-metamorphic growth (Tucker, 1995; Tucker and Phillip, 1995), morphology of newly transformed froglets (Tucker, 1997b); food habits (Tucker, 1997c), and morphological adaptations to fossorial existence (Brown and Means, 1984; Paukstis and Brown, 1987 and 1991). In a previous reports (Tucker and Phillip, 1994 and 1995), we presented preliminary results concerning population size, demography, food habits, activity patterns, and anthropogenic effects on breeding success. We also extended previous observations on distribution of *P. s. illinoensis* in Madison County.

The present report is a summary of results for 1996 and a continuation of studies that we initiated in 1993 and continued in 1994 and 1995 (Tucker and Phillip, 1993; 1994; 1995).

This years activities carried forward objectives from previous years and expanded these to include a detailed analysis of the recently purchase wetland mitigation area. Our initial objectives were:

1. Monitor the distribution of *P. s. illinoensis* choruses in appropriate habitat in the impact area.
2. Estimate the approximate number of *P. s. illinoensis* located on the wetland mitigation area.
3. Determine whether the species is freeze tolerant or not.

Statistical methods

Associations among environmental variables and anuran activity were determined with Spearman's rank correlation (*Rho*). Comparison of means was made using the Kruskal-Wallis test in SAS (SAS Institute, 1988). The sequential Bonferroni method was used to determine minimum values of P needed to reduce the probability of type I errors to 0.05 or less (Rice, 1989).

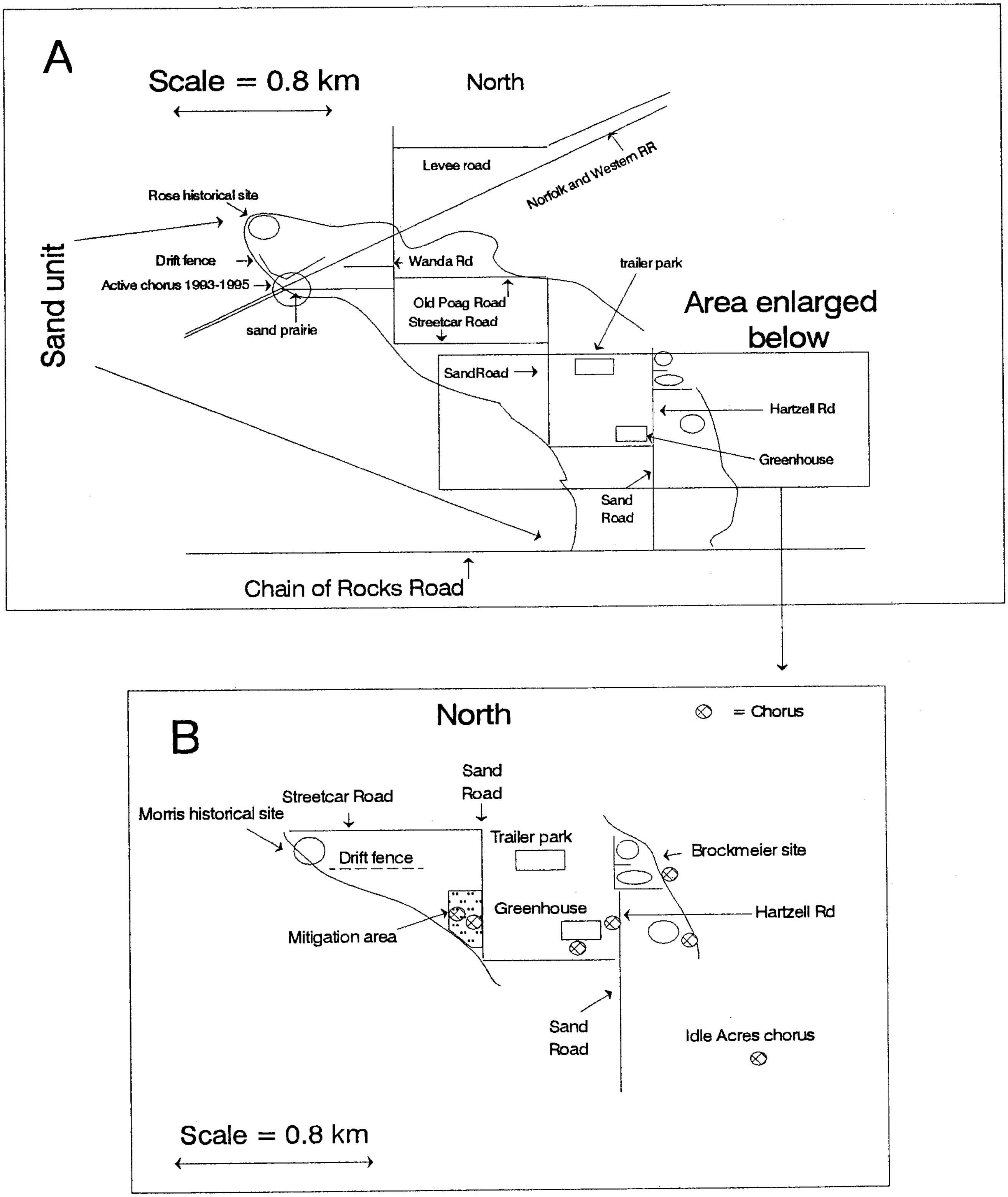
Chorus locations in the Sand Road study area

MATERIALS AND METHODS

Prior to installation of the polygons and drift fences, monitoring of chorus activity was initiated in the Sand Road study area (Fig. 1). The methods used and sites visited were reviewed in previous reports (i.e., Tucker and Philipp, 1993, 1994, and 1995). Monitoring began with the first relatively warm rain of the spring season on 27 February 1996. Suitable conditions (i.e., rainfall with air temperatures above 8°C) also existed on 5 and 14 March and chorus activity was surveyed on those nights as well. Once the drift fences were installed, chorus monitoring occurred nightly until 8 May 1996.

Figure 1. Sand Road study area showing the location of the wetland Mitigation area.

Figure 1


A
Scale = 0.8 km
North
Levee road
Norfolk and Western RR
Rose historical site
Sand unit
Drift fence
Active chorus 1993-1995
sand prairie
Wanda Rd
Old Poag Road
Streetcar Road
trailer park
Area enlarged below
SandRoad
Hartzell Rd
Greenhouse
Sand Road
Chain of Rocks Road
B
North
= Chorus
Sand Road
Streetcar Road
Morris historical site
Trailer park
Brockmeier site
Drift fence
Greenhouse
Hartzell Rd
Mitigation area
Sand Road
Idle Acres chorus
Scale = 0.8 km

RESULTS AND DISCUSSION

In 1996, a total of eight choruses were located (Fig. 1). Seven of these were sites of choruses in previous years. The single new chorus located was on the mitigation site and was located in an excavation that had been made on the site in the summer and fall of 1995.

Chorus sites have been stable in the general study area from 1994-1996 with no indication of recolonization of distant sites where this species is thought to have been extirpated (Tucker and Philipp, 1995; Tucker, 1997d). The use of the newly constructed trench on the Sand Road mitigation site suggests that frogs will adopt newly available breeding sites. Thus, the absence of choruses at former chorus sites is likely due to the inability of frogs to reach those sites from the refugia that they now occupy rather than any behavioral phenomena.

Density Estimates

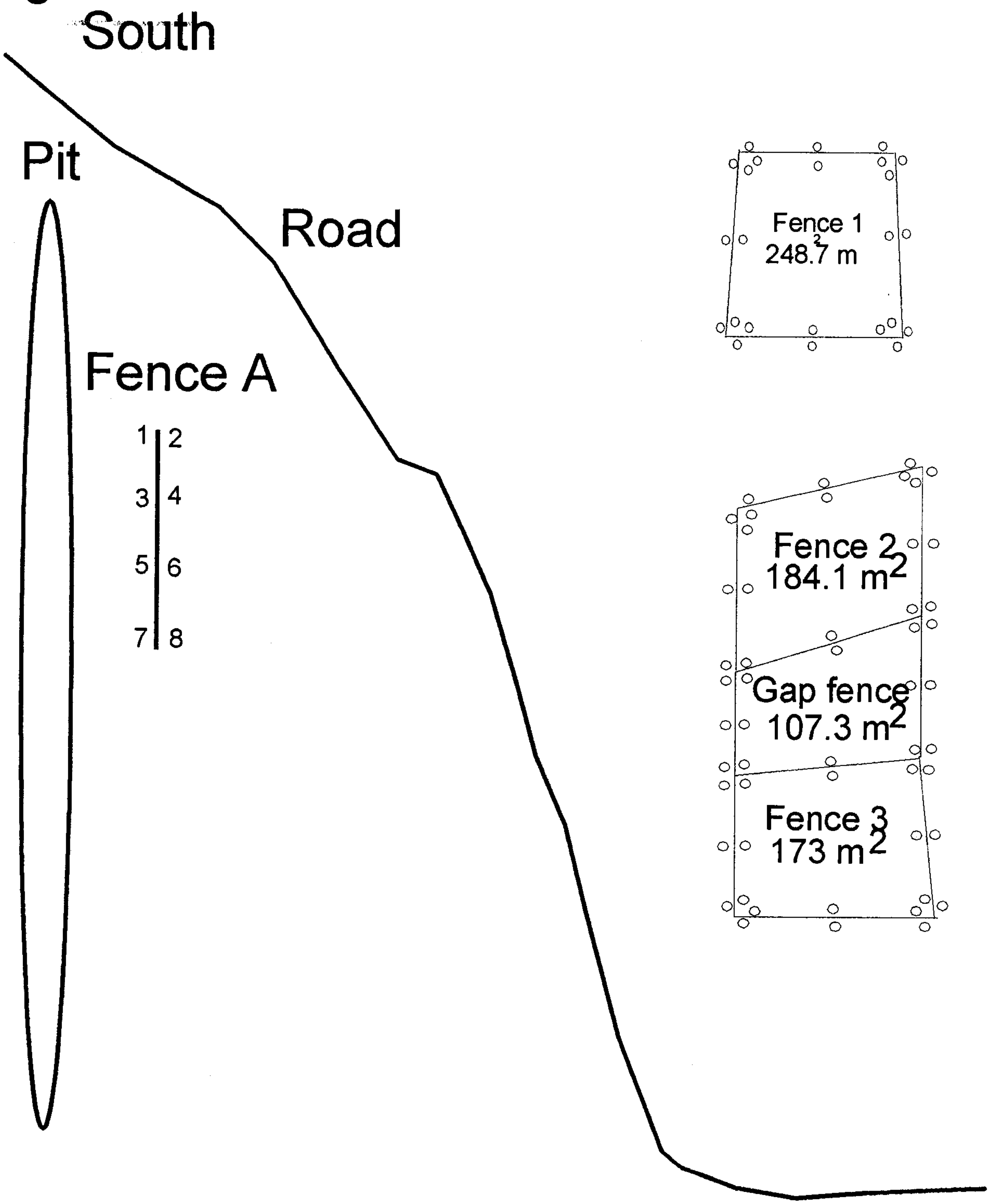
MATERIALS AND METHODS

Drift Fences.-The main objective for this study was to arrive at an estimate of the number of frogs per unit area occupying the study area. To do this, a series of large polygons made of 30 cm aluminum flashing were deployed. The site for each polygon was determined randomly with a grid overlay of the area to be studied using randomly generated pairs of coordinates. Thus, this technique is a modified version of the quadrat method of sampling (Jaeger and Inger, 1994). Three of these randomly determined polygons were placed on the site. Two of the polygons were near each other and the intervening space was closed with flashing to form a fourth polygon (= gap fence). Thus, three polygons abutted each other and were alligned from north to south (Fig. 2).

Each polygon varied somewhat in size with polygon 1 enclosing 248.7 m^2, with polygon 2 enclosing 184.1 m^2, with polygon 3 enclosing 173 m^2, and with the gap polygon enclosing 107.3 m^2 (Fig. 1). Three pitfall traps were placed along both sides of each side of each polygon (Fig. 2, Fence 1 for example).

Figure 2. Detail of wetland mitigation area showing location and construction of polygons.

Figure 2


South
Pit
Road
Fence A
1
2
3
4
5
6
7
8
Fence 1
248.7 m2
Fence 2
184.1 m2
Gap fence
107.3 m2
Fence 3
173 m2

A 45 m long drift fence was also placed near an existing excavation. This fence had six pitfall traps on each side and was alligned from north to south. The site was selected because it lay between much of the suitable habitat on the site and the excavation that was expected to be a breeding site. This fence was the only transect sampling fence (i.e., Jaeger, 1994) deployed. The outer sides of the polygons, however, also represent transect sampling devices but differ because they were in homogeneous sites (Jaeger, 1994).

All polygons and the 45 m drift fence were constructed between 22 and 23 March 1996. They were monitored at least once daily. During periods of maximal anuran activity they were monitored several times per 24 h period. Monitoring continued until 14 June 1996.

Collection of animals.-Most animals were found in pitfall traps or along the flashing between pits. The time, date, pit number, and location within each polygon was recorded for each animal. All anurans were marked by toe clipping and released shortly after collection. Each animal was released on the opposite side of the fence from the pit of collection. In some instances, individuals were released into polygons. Recaptures of individuals leaving polygons after being released into polygons were differentiated from those of individuals not marked on the outer border of a particular polygon. All newly transformed *Pseudacris s. illinoensis* were given the same year specific cohort marking for later recognition. The number of frogs remaining in polygons was calculated by subtracting the number of frogs recorded leaving polygons from the number of frogs placed into polygons.

Snout-to-vent length (SVL) was recorded for each anuran to the nearest 1 mm. Sex was determined by examining secondary sexual characteristics and was recorded at the time of collection. If eggs could be seen through the body wall of females they were recorded as gravid. If eggs could not be seen but females were large enough to be mature they were recorded as spent. Anurans smaller (i.e., newly transformed froglets) than known minimal sizes at maturity were recorded as juveniles. Animals other than anurans were removed from pits, their identification recorded, and then released shortly afterwards.

The excavation located on the site did eventually become a chorus site for several species of anurans. Anurans were collected there each night after chorusing began. These frogs were also marked, measured, and released.

RESULTS AND DISCUSSION

A total of 199 anuran amphibians as well as other mammals and reptiles were collected on drift fences and at choruses on the study site (Table 1). Anurans were caught primarily along the drift fences but about one-quarter of the total anurans examined were collected at a chorus on the site (Table 2). Three additional specimens of *Pseudacris streckeri illinoesis* were collected on Sand Road that bordered the study site and were not included in the tables.

Anurans caught along drift fences included specimens of males and females in about equal numbers (Table 3). In contrast collections made at the chorus were heavily male biased (Table 4). Most anurans caught appeared to be adults based on possession of secondary sexual characteristics among males and size or oviductal eggs among females. For species where juveniles were collected (Table 3), juveniles were less commonly collected than adults for the two species of *Bufo*. Only juvenile *Rana catesbiana* were collected.

Sexual size dimorphism was apparent in some of the anurans collected (Table 5). Statistical comparison of SVL for males vs. females were made for *Bufo woodhousii fowleri* (KW = 11.72, $p = 0.0006$); *Hyla versicolor* (KW = 3.05, $p = 0.0808$); *Pseudacris triseriata* (KW = 24.8 $p < 0.0001$); and *P. s. illinoensis* (KW = 5.29, $p = 0.0214$). Except for the small sample of *Hyla versicolor*, females averaged larger than males in SVL for the other three species (Table 5).

The distribution of anurans on the various drift fences was variable with more anurans being caught on the west side of the three conjoined polygons.

Table 1. All animals collected by all means between 23 March and 8 May, 1996.

Mammals	
Blarina carolinensis	2
Peromyscus maniculatus	4
Microtus ochrogaster	6
Total Mammals	12
Reptiles	
Lampropeltis calligaster	2
Chrysemys picta	9
Cnemidophorus sexlineatus	3
Total Reptiles	14
Anurans	
Rana blairi	2
Rana catesbiana	3
Rana sphenocephala	3
Bufo americanus	6
Bufo woodhousii fowleri	63
Hyla versicolor	14
Pseudacris triseriata	67
Pseudacris streckeri illinoensis	41
Total Anurns	199

Table 2. Location of anuran captures.

Species	Drift fences	Chorus
Rana blairi	2	0
Rana catesbiana	3	0
Rana sphenocephala	3	0
Bufo americanus	4	2
Bufo woodhousii fowleri	35	28
Hyla versicolor	4	10
Pseudacris triseriata	64	3
Pseudacris streckeri illinoensis	39	2
Total	154	45

Table 3. Males, females, and juveniles collected on drift fences for each anuran species with number of gravid females in parentheses.

Species	Females	Juveniles	Males
Rana blairi	2(1)	0	0
Rana catesbiana	0	3	0
Rana sphenocephala	0	0	3
Bufo americanus	1	1	2
Bufo woodhousii fowleri	6(2)	14	15
Hyla versicolor	1	0	3
Pseudacris triseriata	31(11)	0	33
Pseudacris streckeri illinoensis	21(9)	0	18
Total	62(23)	18	74

Table 4. Sex of anurans caught at breeding chorus with number of gravid females in parentheses.

Species	Females	Males
Bufo americanus	1	1
Bufo woodhousii fowleri	3(3)	25
Hyla versicolor	1(1)	9
Pseudacris triseriata	0	3
Pseudacris streckeri illinoensis	0	2
Total	5(4)	40

Table 5. Comparison of snout-to-vent length (in mm) for males, females, and juveniles of selected anurans caught on drift fences and at choruses.

Species	Females Mean(SD)/range	Males Mean(SD)/range	Juveniles Mean(SD)/range
Bufo woodhousii fowleri	62.3(5.85)/54-73	54.5(4.47)/47-66	43.6(6.30)/36-54
Hyla versicolor	51.0(5.66)/47-55	44.5(4.42)/38-54	---
Pseudacris triseriata	31.9(2.13)/27-36	29.1(1.70)/26-33	---
Pseudacris s. illinoensis	40.5(2.79)/35-44	38.6(2.58)/32-42	---

Sample sizes are given in Table 3.

Fence A also tended to catch more anurans on the west side of the fence (i.e., 37 on the west side of the fence and 22 on the east side of the fence, Fig. 3). However, polygon 1 had about equal numbers of frogs caught on the east and west sides of the fence but fewer on the north and south sides of the fence (Fig. 3).

In all, 18 specimens of 5 species of anurans were initially encountered inside one of the four polygons (Table 6). Two of these species (*Hyla versicolor* and *Rana sphenocephala*) may have been caught after they entered polygons because the former could easily climb the flashing using their sticky toe pads and the latter could have leaped over the fences due to their relatively large size and well developed leaping ability. Consequently, they were not considered further except to note that density estimates for *Hyla versicolor* averaged 0.004 frogs/m^2 and for *Rana sphenocephala* it was 0.003 frogs/m^2.

The other three species (*B. w. fowleri*, *P. triseriata*, and *P. s. illinoensis*) were considered unlikely to have entered the polygons undetected but were likely present in the area enclosed by the polygons prior to their construction. Consequently, these captures were used to estimate the density per unit area for these three species on the site. For *B. w. fowleri*, three specimens were initially captured inside polygons (one in Polygon 3 and 2 in Polygon 1). The mean density estimate based on these three specimens was 0.0035 toads per m^2 (range = 0.008-0 toads/m^2, n = 4 polygons). *Pseudacris triseriata* was the most frequently caught anuran inside polygons with 11 specimens being recovered among the four polygons (3 inside Polygon 1, 5 inside Polygon 2; 2 inside Polygon 3, and 1 inside Gap polygon). These captures yielded an estimated density of 0.015 frogs/m^2 (range = 0.009-0.027 frogs/m^2, n = 4 polygons). A single specimen of *P. s. illinoensis* was found inside Polygon 1 yielding a density estimate for this species of 0.001 frogs/m^2 (n = 4 polygons).

Figure 3. Number of anurans caught on drift fences in the study area for each fence. The number on the left side of each slash is the total number of anurans caught; the number on the right side of each slash is the number of *Pseudacris streckeri illinoensis* caught.

Figure 3

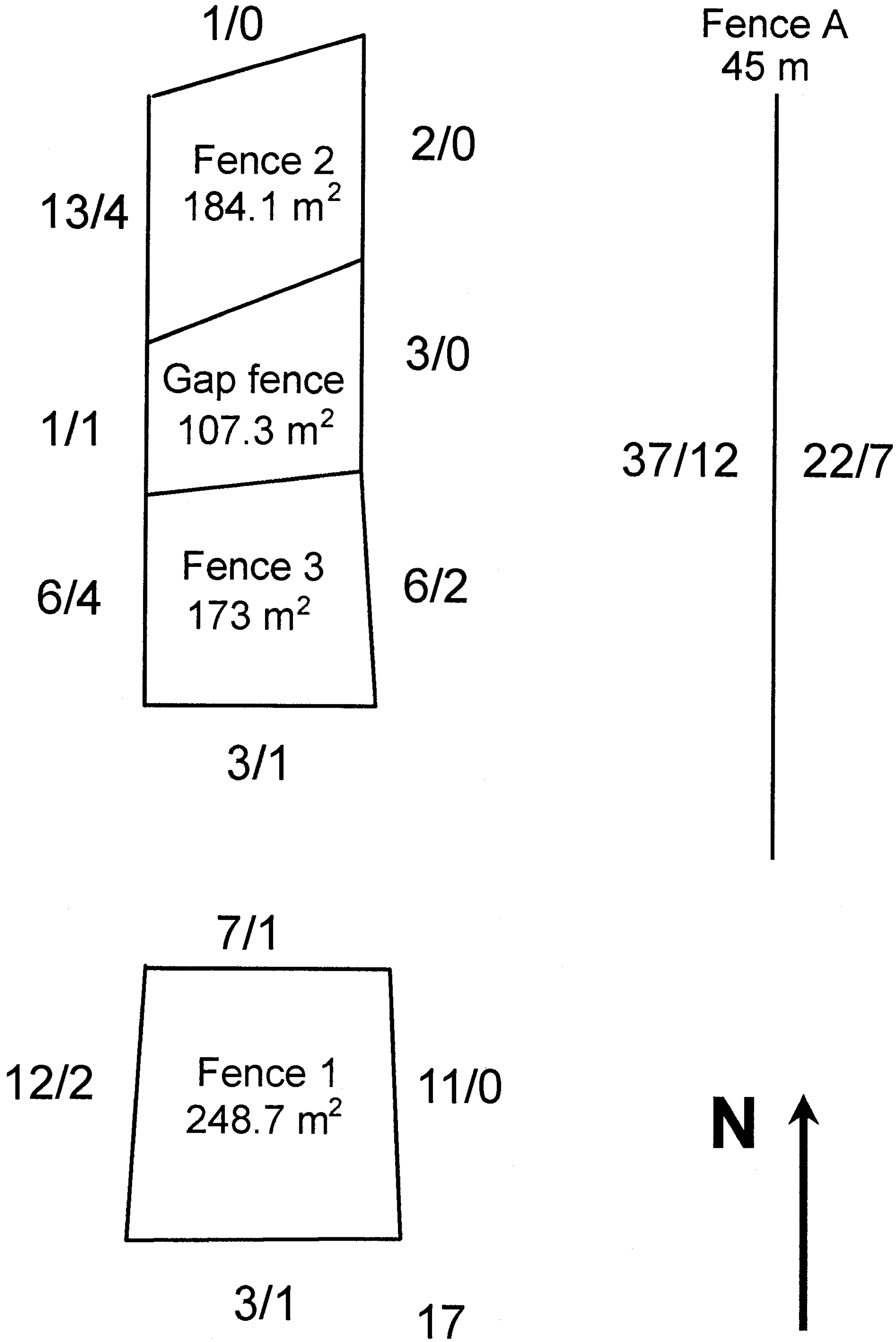

1/0
Fence A
45 m
2/0
Fence 2
184.1 m²
13/4
3/0
Gap fence
107.3 m²
1/1
37/12
22/7
Fence 3
173 m²
6/4
6/2
3/1
7/1
Fence 1
248.7 m²
12/2
11/0
N
3/1
17

Table 6. Location of anuran captures for each drift fence polygon.

	Fence 1		Fence 2		Fence 3		Gap fence	
Species	outer	inner	outer	inner	outer	inner	outer	inner
Rana blairi	1	0	0	0	0	0	0	0
Rana catesbiana	2	0	0	0	0	0	0	0
Rana sphenocephala	2	0	0	0	0	0	0	1
Bufo americanus	0	0	0	0	2	0	0	0
Bufo w. fowleri	8	2	6	0	4	1	1	0
Hyla versicolor	1	0	0	0	0	1	0	1
Pseudacris triseriata	14	3	7	5	7	2	2	1
P. s. illinoensis	4	1	4	0	7	0	1	0

Captures for Fence A are not included in these totals.

The estimates of density roughly paralelled the total number of captures made on drift fences (Table 2). *Pseudacris triseriata* was the most commonly collected species and had the highest density estimate. In contrast, *P. s. illinoensis* was the least commonly collected of the three species and had the lowest density estimate (Table 2).

Overall 142 newly transformed froglets of *Pseudacris streckeri illinoensis* were caught on the study area. All froglets were caught on either the east or west side of the drift fence or polygons. Most froglets apparently transformed from the chorus on the far western edge of the study site because 93 of 142 froglets were caught on the west side of the fences. However, 39 froglets were caught on the east side of the drift fence arrays suggesting that breeding was successful in the newly excavated trench. All froglets averaged 20.9 mm in SVL.

Froglets caught on the outer side of the polygons were initially placed within polygons after they were marked. In all, 23 froglets were not recaptured leaving those polygons suggesting that they remained within the polygons. Density estimates for froglets remaining in the polygons were 0.036 froglets/m^2 for polygon 1, 0.033 froglets/m^2 for polygon 2, 0.029 froglets/m^2 for polygon 3, and 0.028 froglets/m^2 for the gap polygon. Average density estimate for froglets remaining within polygons was 0.032 froglets/m^2 ($n = 4$ polygons).

Similarly, three adult frogs that were placed within polygons were not found leaving them. Two of these appeared to have remained in polygon 1 and one in polygon 2. Density estimates for adult frogs remaining in polygons were 0.008 frogs/m^2 for polygon 1 and 0.005 frogs/m^2 for polygon 2. All other frogs entering polygons were recaptured as they left them. Average density of adult frogs remaining within the four polygons was 0.003 frogs/m^2 or 30 frogs per h.

Population size estimates

MATERIALS AND METHODS

Two estimates of population size were made. The first used the density estimate derived from captures inside polygons multiplied by the area of suitable sand habitats on the study area to arrive at a population size estimate. The coverage of suitable sand habitats was estimated from aerial photographs of the study site and was estimated at 7.1 h.

A second population size estimate was made using the Petersen method as modified by Bailey (1951) for estimates of population size when number of recaptures were small (Donnelly and Guyer, 1994). Standard error of these estimates was calculated using Bailey's (1951) method. Estimates were calculated for males and females separately based on the total number of frogs marked in 1996 and the total number of frogs recaptured in 1996. Recaptures of frogs crossing polygons were excluded.

Population size was also estimated using the same method for area wide captures of frogs marked in 1994 and recaptured in 1995 (Tucker and Philipp, 1995). Although previously used for population estimates (Tucker and Philipp, 1995), population size was recalculated using the Bailey (1951) method to make them more comparable to estimates based on 1996 data.

RESULTS AND DISCUSSION

Assuming that about 7.1 h of suitable sand habitat existed at the study area, then the density estimate of 0.001 *Pseudacris streckeri illinoensis*/m^2 would suggest that 71 frogs should be expected to occupy this area. This was based on an estimate of 10 frogs per h from density estimates. In contrast, estimates for *Bufo woodhousii fowleri* would be 35 toads per h and for *Pseudacris triseriata* it would be 150 frogs per h.

In contrast, three times as many adult frogs may have remained within polygons as were captured leaving them. If as many frogs remained in other similar areas on the study site, then population size estimate would be 213 frogs occupying the site (i.e., 30 frogs per h). In contrast to the single female found leaving a polygon, two of three frogs thought to have remained in polygons were males and one was a female.

Assuming that froglets remaining within polygons typified the density on the site overall, then an estimate of the number of froglets entering the site in 1996 can be made. Average density estimate was 320 froglets per h for a total of 2272 froglets entering the site in 1996.

Petersen estimates of population size were 99 ± 18.9 frogs for females and 80 ± 16.2 frogs for males based on 3 recaptures of 18 marked females and 5 recaptures of 20 marked males. Thus, a rough population estimate overall would be about 179 individual adult *P. s. illinoensis*. Population estimates of the other two species were not made for this report.

Recaptures were also made of froglets initially marked on one fence array and found on another (i.e., those not simply leaving a polygon). However, only a single froglet initially marked on the west side of polygons was recaptured on the west side of Fence A and only a single froglet initially marked on the east side of Fence A was later recaptured on the east side of the polygon fences. These two recaptures suggested that about 922 froglets and 295 froglets left the breeding sites on the west and east sides of the study area, respectively. Thus, estimate of number of froglets would be the sum of these two figures for a total of about 1217 froglets moving about the study area.

The density estimate (i.e., 71 animals) was much less that the population estimate based on mark-recapture results. In part, the discrepancy likely is due to error inherent to the two estimates. However, we know that frogs living outside the mitigation area migrate to the mitigation area to breed there (Tucker and Philipp, 1995 and 1996). This influx of frogs from elsewhere to breed on the site would be accounted for in the mark-recapture estimate but not in the denisty estimate. Our results suggest that not only is the mitigation area important as a nonbreeding habitat but it is apparently a critical resuorce for frogs that live elsewhere. Consequently wetland restoration will have a wider impact on the entire area than suggested by the small number of frogs found using drift fence polygons.

Environmental correlates of anuran activity

MATERIALS AND METHODS

Soil and air temperatures were recorded each time the drift fences were checked even when more than one check per 24 h was made. Both measurements were made with Reo-Temp thermometers. Air temperature was measured at 25 cm and soil temperature at 20 cm soil depth. A rain gauge was installed in polygon 1 and was read each time the fences were monitored.

RESULTS AND DISCUSSION

The large number of captures with associated environmental parameters allowed an examination of the relationship of frog activity as reflected by the number of frogs caught per fence check and environmental measures of air and soil temperature and precipitation. Anurans were divided into three classifications including specimens of *P. triseriata, P. s. illinoensis*, and all other anurans (i.e., Table 2 and primarily *B. w. fowleri*). The association (Spearman's *Rho*) between these three categories and the three environmental parameters were determined (Table 7).

Environmental variables differed in their relationships to the number of each anuran category examined. Anuran activity was closely related to soil temperatures for all three categories (Fig. 4), whereas no statistically significant associations occurred between the number of each anuran category caught and air temperature (Fig. 5, Table 7). The response to rainfall varied among classifications (Fig. 6). The number of *Pseudacris triseriata* and other anurans combined was associated with precipitation, whereas the number of *P. s. illinoensis* was not related to precipitation.

Because environmental variables were associated with each other, partial correlation was used to remove the effect of precipitation on air and soil temperatures and to remove the effect of air and soil temperatures on precipitation. The associations developed by partial correlation were

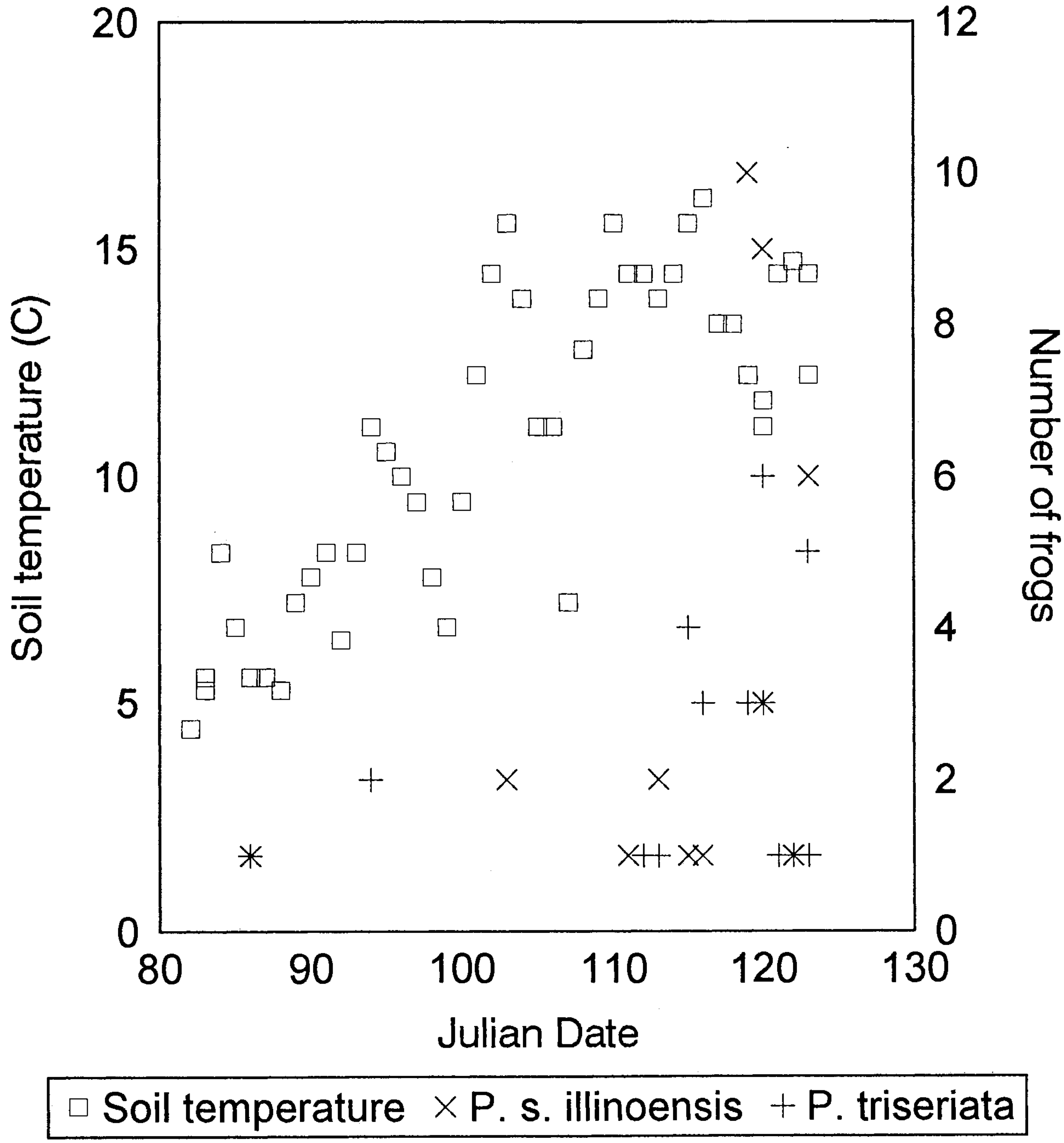
Table 7. Association between environmental variables and number of frogs captured on drift fences.

	TEMPERATURE					
	SOIL		AIR		PRECIPITATION	
Species	*Rho*	*p*	*Rho*	*p*	*Rho*	*p*
Pseudacris s. illinoensis	0.41	0.0020	0.14	0.3017	0.30	0.0290
Pseudacris triseriata	0.44	0.0008	0.32	0.0170	0.39	0.0040
Other anurans	0.39	0.0034	0.24	0.0832	0.43	0.0010
Partial Precipitation						
Pseudacris s. illinoensis	0.40	0.0033	0.13	0.3355	---	---
Pseudacris triseriata	0.43	0.0012	0.33	0.0157	---	---
Other anurans	0.38	0.0050	0.24	0.0823	---	---
Partial Soil/Air						
Pseudacris s. illinoensis	---	---	---	---	0.27	0.0495
Pseudacris triseriata	---	---	---	---	0.38	0.0058
Other anurans	---	---	---	---	0.43	0.0017

For all comparisons number of drift fence checks is 54. Values of $P > 0.006$ should be viewed with caution due to the large number of comparisons.

Figure 4. Relationship between soil temperature and activity in two species of *Pseudacris*.

Figure 4



Soil temperature (C)
Number of frogs
Julian Date
20
15
10
5
0
12
10
8
6
4
2
0
80
90
100
110
120
130
Soil temperature
P. s. illinoensis
P. triseriata

Figure 5. Relationship between air temperature and activity in two species of *Pseudacris*.

Figure 5

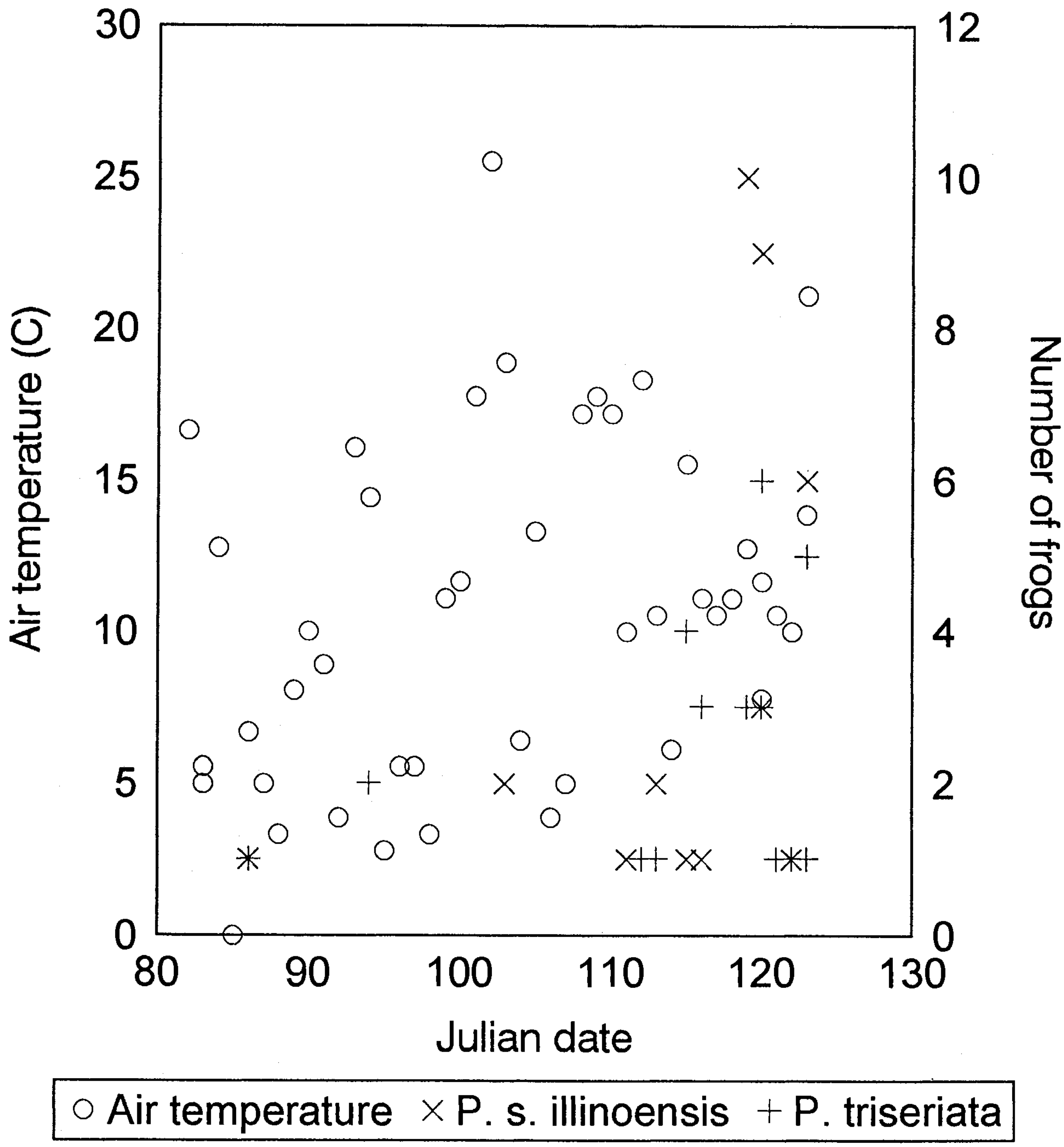
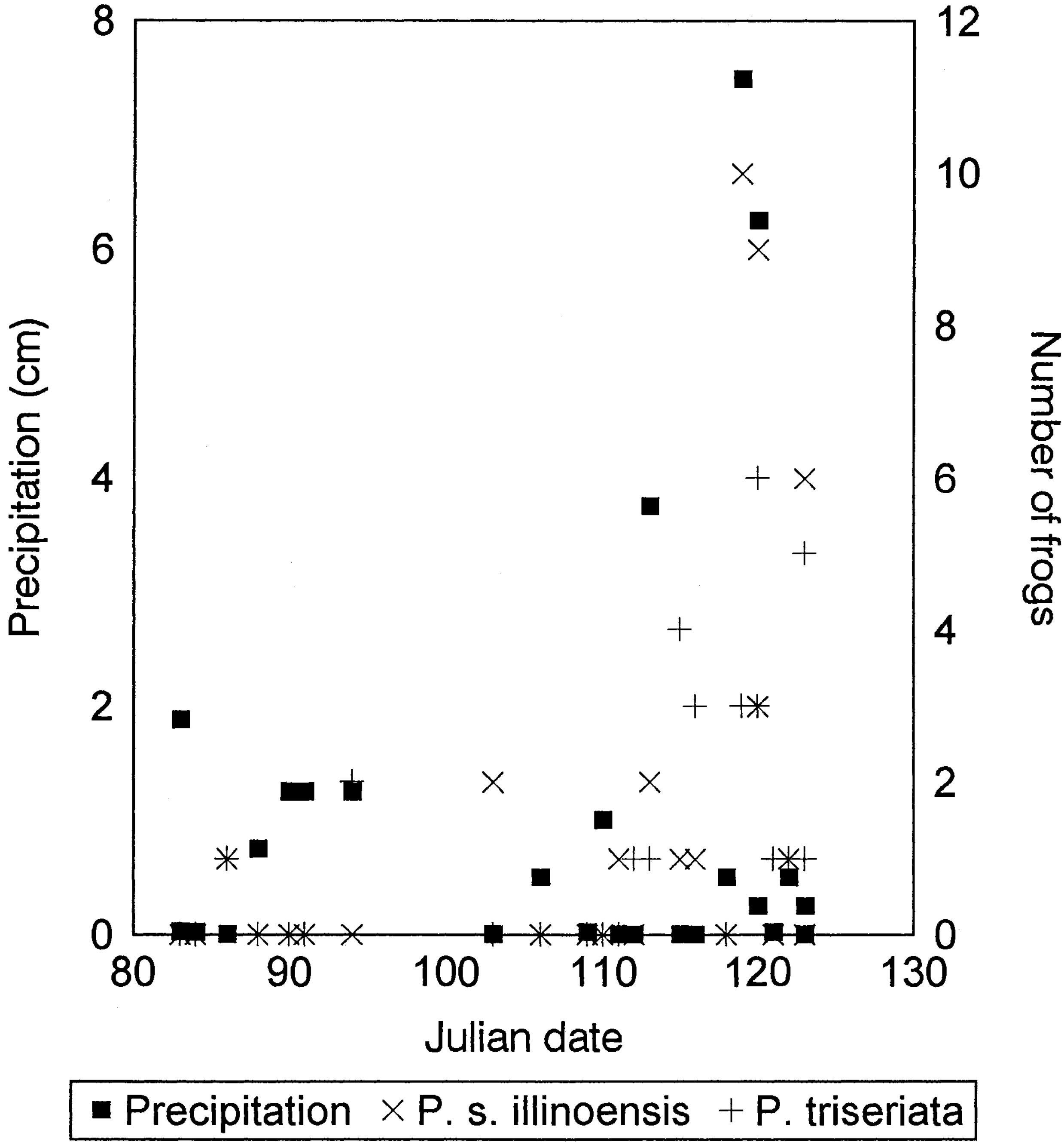

Air temperature (C)
Number of frogs
Julian date
30
25
20
15
10
5
0
12
10
8
6
4
2
0
80
90
100
110
120
130
○ Air temperature
× P. s. illinoensis
+ P. triseriata

Figure 6. Relationship between precipitation and activity in two species of *Pseudacris*.

Figure 6



Precipitation (cm)
Number of frogs
Julian date
0
2
4
6
8
10
12
80
90
100
110
120
130
Precipitation
P. s. illinoensis
P. triseriata

essentially identical to those described above. Soil temperature was still closely associated with activity of all three classifications of anurans. In contrast, air temperature was not associated with anuran activity. Rainfall absent the possible effect of air and soil temperatures was still associated with activity of *P. triseriata* and the other anurans collected but not with the activity of *P. s. illinoensis*.

Invertebrate sampling

MATERIALS AND METHODS

Invertebrates were collected from pitfall traps along drift fences between 23-27 March 1996. These collections were made to judge the number and types of prey items that might typically be available to *P. s. illinoensis* during its breeding migration at the study site. Insects were identified to order (Borror et al. 1989).

RESULTS AND DISCUSSION

The 1996 invertebrate collections from pitfall traps would underestimate the frequency of more mobile insects such as dipterans and overestimate the frequency of less mobile insects such as lepidopteran larvae (Table 8). Nonetheless of the 286 lepidopteran larvae collected, 271 were larval cutworms (Noctuidae). Noctuid larvae were the most abundant potential food source among less mobile invertebrates collected.

The 1996 invertebrate collections and food items found in frogs collected in 1994 (see Tucker and Philipp, 1996; Tucker, 1997c and Table 8) were rather similar considering that pitfall traps intended to capture frogs would underestimate the frequency of more mobile insects such as dipterans and overestimate the frequency of less mobile insects such as lepidopteran larvae (Table 8). Of the 286 lepidopteran larvae collected, 271 were larval cutworms. Although insect collections were not concurrent with the food habits study, they suggest that *P. s. illinoensis* is an opportunistic predator. The large number of noctuid larvae found in stomachs of *P. s. illinoensis* in 1994 likely reflected the abundance of the cutworms at the site

Table 8. Comparison of stomach contents of *Pseudacris streckeri illinoensis* collected in 1994 (data from Tucker and Philipp, 1994) to invertebrates collected in pitfall traps in 1996.

	From frog stomachs		From pitfall traps	
Kind of invertebrate	N	% of all items	N	% of all items
Arachnid	3	6.8	24	6.8
Hemiptera	4	9.1	14	4.0
Coleoptera	8	18.2	22	6.3
Diptera	5	11.4	0	0.0
Lepidoptera	22	50.0	286	81.5
Hymenoptera	2	4.5	1	0.3
Orthoptera	0	0.0	4	1.1

and not selective predation on cutworms.

Freeze Tolerance

MATERIALS AND METHODS

Experimental organisms.-Male specimens of two chorus frogs, including the western chorus frog (*Pseudacris triseriata*) and the Illinois chorus frog (*Pseudacris streckeri illinoensis*) were used for this experiment. Specimens were collected between 25 and 28 April 1996. Specimens of both species were collected under Illinois Department of Natural Resources permit #96-4S. Surviving specimens of *P. triseriata* were released at the collecting location. Specimens that failed to survive were deposited as voucher specimens in the Illinois Natural History Survey (INHS 12912-12919, 12353) and the Colorado State University teaching collection (CSU uncataloged). Experimental work was performed in the laboratory of Gary C. Packard (Colorado State University, Fort Collins, Colorado).

Experimental protocol. Frogs of both species were received at the laboratory at Colorado State University on 30 April 1996. Both species were housed separately in plastic containers. These enclosures contained a shallow pool of water, but no food was offered. Containers were kept in an environmental chamber at 3°C until 29 May 1996 when experiments were initiated.

Before testing, each frog was blotted dry to remove excess moisture from the skin and pressure was applied to the abdomen to expel fluid from the bladder. A copper-constantan thermocouple was then placed into a pyrex test tube after which the frog was inserted so that the thermocouple was in contact with the ventral side of the frog during the experiment. Ventral temperatures were recorded continuously. A piece of foam was inserted over the frog for insulation and to prevent movement by the frog. The resulting apparatus was then placed in a water bath at 0.6°C. This temperature was maintained for 30 min to allow the body temperature of the frog to equilibrate with the ambient temperature. After equilibrium was reached, the temperature of the water bath was lowered to 0°C. This temperature was maintained for one h. The foam plug was then removed and ice was placed on the dorsum of the frog to initiate ice formation in the body fluids. The temperature was then immediately lowered to -1°C. After the ice was added, the frog was left in the water bath for 24 h. After each trial, the frogs were allowed to warm to room temperature for 24 h at which time survival was assessed. In all, nine specimens of *P. s. illinoensis* and eight specimens of *P. triseriata* were tested. Survivorship between species tested for freeze tolerance was compared using Fisher's exact test in SAS (SAS Institute, 1988).

Soil temperatures. Soil temperatures were recorded at the Sand Road site during the winter of 1996/1997 using ten HOBO-XT temperature loggers (Onset Computer Corporation). Temperature monitoring began on 16 December 1996 and was terminated on 21 February 1997, the date that *Pseudacris s. illinoensis* were first found active on the soil surface in 1997.

Loggers were placed in pairs with one thermocouple probe of each pair inserted into the sand at a depth of 12.5 cm and the other at 25 cm. Before each logger pair was placed the percentage of the general site covered by vegetation was estimated. Probes were then inserted by pushing them into the sides of a larger vertical shaft where the two loggers were placed. The logger and probes were then reburied. Loggers recorded temperature readings every 3.67 hours during the duration of deployment. Thus, each logger recorded 503 temperature readings during the period of deployment. Overall 2515 temperature readings were recorded at each depth. Means listed below are accompanied by ± one standard deviation.

We compared temperatures recorded using the Kruskal-Wallis test. Comparisons were made for each pair of loggers (i.e., shallow vs. deep for all five pairs, degrees of freedom = 1 for each test) and among all shallow or all deep loggers (degrees of freedom = 4 for both comparisons). Because we performed seven Kruskal-Wallis tests, the minimum value of P that reduces the probability of a type I error to less than 0.05 was 0.0071 (Rice, 1989).

RESULTS AND DISCUSSION

Experimental results. All frogs of both species froze after ice was placed into contact with them as demonstrated by a freezing exotherm in the temperature profiles recorded for each frog (Fig. 7). Animnals froze to a thermal equilibrium wityh their environment withim 4-5 h, at which point another change in slope was apparent in the temperature profile and temperature tracing became essentially horizontal (Fig. 7). Minimum temperature for frogs varied from -1.2°C to -1.6°C, but did not differ significantly between species ($F_{1,15}$ = 2.94, P = 0.11; grand mean = -1.25°C).

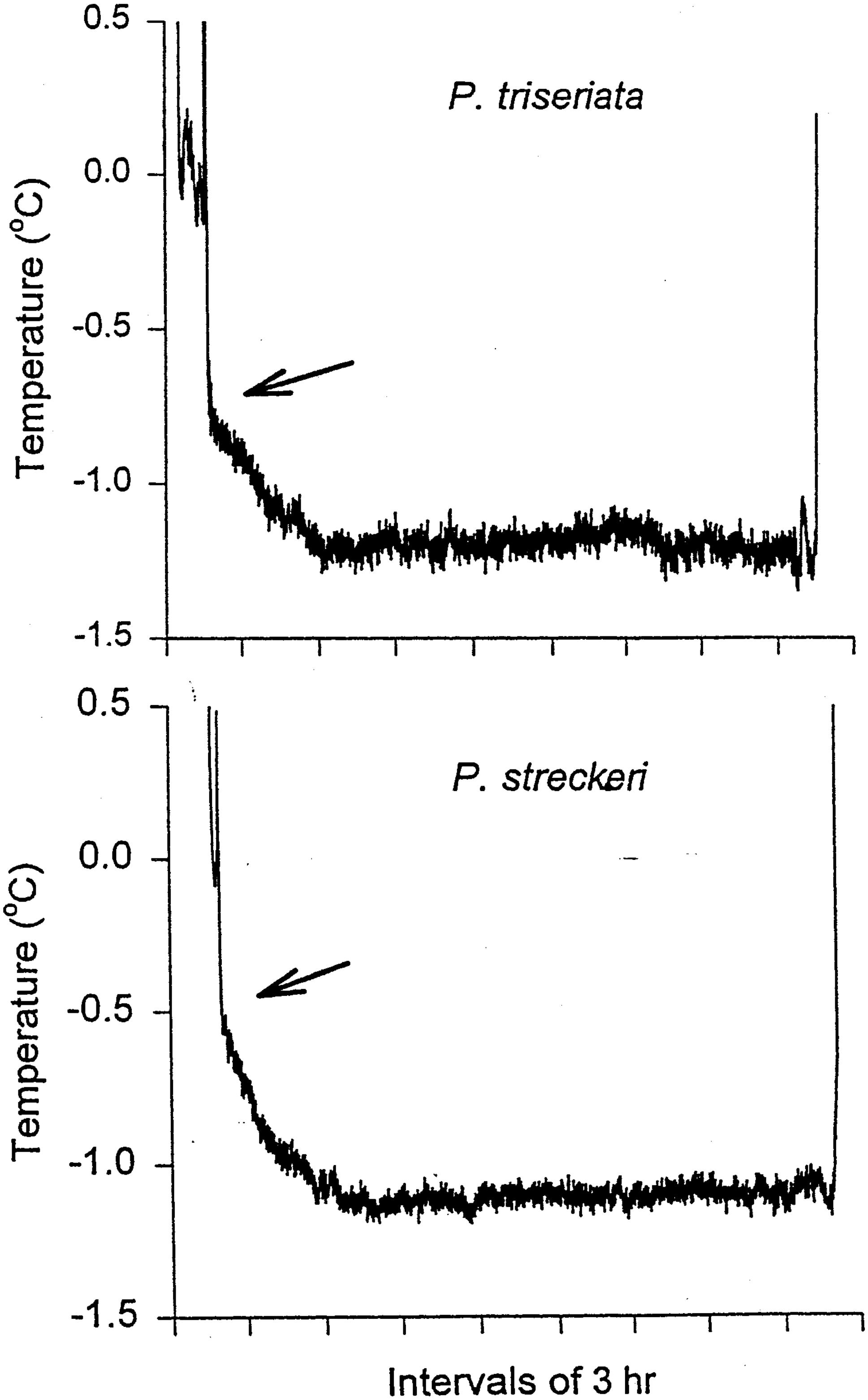
Despite suffering at least some degree of tissue freezing, all eight of the *P. triseriata* survived the experimental protocol. In contrast, only one of nine individual *P. s. illinoensis* survived the experimental protocol. This individual died a few days later, whereas all of the *P. triseriata* survived to be released about fourteen days after the experimental protocol was conducted.

Survivorship of *P. triseriata* was significantly greater than survivorship of syntopic *P. s. illinoensis* (Fishers exact χ^2 = 14.4, P = 0.0004). These results suggested that *P. triseriata* was able to survive at least some tissue freezing despite being unable to resist inoculative freezing. *Pseudacris s. illinoensis*, however, failed to survive inoculative freezing of tissues and cannot be said to be be freeze tolerant. Thus, when exposed to subfreezing temperatures in the presence of ice, most individual *P. s. illinoensis* can be expected to die. The results of these experiments were consistent with the hypothesis that *P. s. illinoensis* was less tolerant of exposure to subfreezing temperatures when ice was present than was syntopic *P. triseriata*.

Field results. All logger pairs were consistent in that each member of the pair differed significantly from the other (P < 0.0001). In each instance, the mean temperature at 25 cm was higher than the mean temperature at 12.5 cm during the period when loggers were deployed. Overall, mean temperature at 25 cm was 2.84 ± 2.32°C (range = -0.06-11.96°C) compared to a mean temperature of 2.28 ± 3.02°C (range = -3.05-14.62°C) at 12.5 cm. Readouts for a typical

Figure 7. Temperature profiles of two species of *Pseudacris* exposed to freezing temperatures.

Figure 7


0.5
0.0
-0.5
-1.0
-1.5
Temperature (°C)
P. triseriata
0.5
0.0
-0.5
-1.0
-1.5
Temperature (°C)
P. streckeri
Intervals of 3 hr

logger pair are shown in Fig. 8. There was variation in mean temperature among loggers at each depth ($P < 0.0001$).

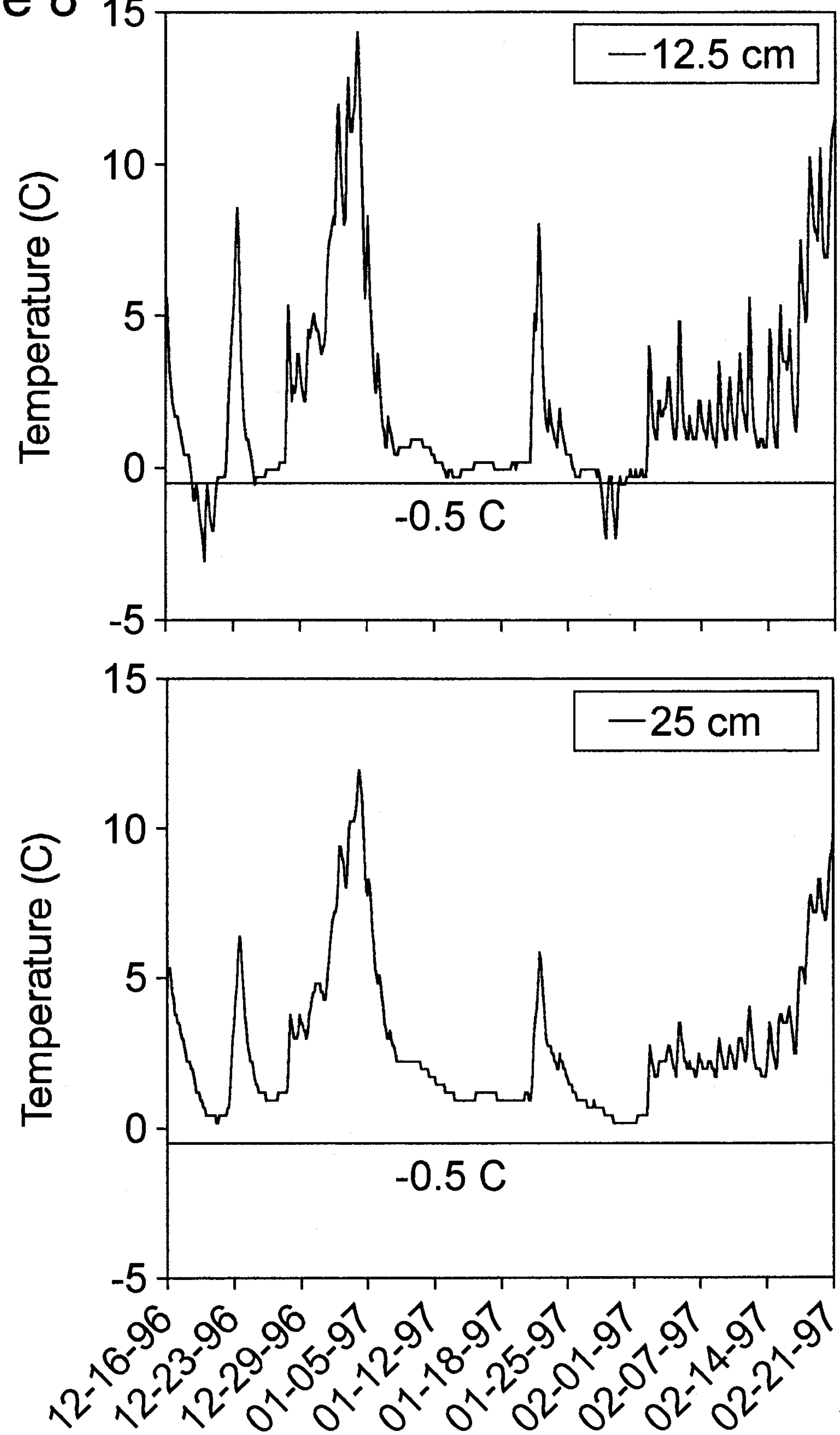
However, mean temperatures may be less important biologically than the low end of the range recorded at each depth because subfreezing temperatures were potentially life threatening for *Pseudacris s. illinoensis*. Among the five loggers at 12.5 cm, all recorded periods where the soil temperature was less than 0°C. The lows for these five loggers ranged from -0.56 to -3.05°C. In each case, subfreezing temperatures were recorded for longer than 24 h during one or more periods in the time the loggers were deployed (i.e., Fig. 8). In contrast, lows for the five loggers at 25 cm ranged from -0.06-0.43°C. Only one logger recorded temperatures below 0°C. The subfreezing temperatures recorded by this logger persisted for about 12 h on a single day during the time the loggers were deployed. Excepting these readings, all other temperature readings at 25 cm were above 0°C.

Overall, we found no statistically significant association between percent vegetation cover and mean temperature (Rho = 0.12, $P = 0.73$, N = 10 sensors), minimum temperature (Rho = 0.22, $P = 0.54$, N = 10 sensors), or maximum temperature (Rho = -0.23, $P = 0.51$, N = 10 sensors). Nor did we find any significant associations between percent vegetation cover and temperature variables among the five sensors set at 125 mm or the five set at 250 mm. However, in each case, the association between percent vegetation cover and maximum temperature measured was negative whereas it was positive between percent vegetation cover and minimum temperature recorded and mean temperature recorded. Tentatively, we conclude that if all other factors are equal that reducing vegetation cover percentage will tend to reduce the mean temperature and the maximum temperature at a particular site during the winter. However, reducing percent vegetation cover would tend to increase the minimum temperature that overwintering frogs are subjected to.

Presumably, the above result, though highly tentative due to small number of sensors available, is due to solar warming acting in concert with the

Figure 8. Temperature profiles for soil during the winter of 1996/1997.

Figure 8



12.5 cm
25 cm
Temperature (C)
-0.5 C
15
10
5
0
-5
12-16-96
12-23-96
12-29-96
01-05-97
01-12-97
01-18-97
01-25-97
02-01-97
02-07-97
02-14-97
02-21-97

insulative properties of the soil. Most importantly, we find no evidence that reducing vegetative cover will increase the risk of freezing during overwintering. This is important because use of fire to help restore native sand prairie vegetation and proposed activities to recreate and rehabititate wetland habitats will result in reduced vegetation cover.

Thermobiology of *Pseudacris streckeri illinoensis* in relation to other anurans. Anurans seem to utilize one of two physiological strategies to survive winter temperature extremes in temperate climates. Some species are able to supercool but are not freeze tolerant (e.g., *Bufo americanus*-Storey and Storey, 1986; *Scaphiopus bombifrons*-Swanson and Graves, 1995), whereas others supercool and are freeze tolerant (e.g., *Rana sylvatica*-Schmid, 1982; Storey and Storey, 1986; Layne et al., 1990; *Pseudacris triseriata*-MacArthur and Dandy, 1982; Storey and Storey, 1986; *Pseudacris crucifer*-Schmid, 1982; Storey and Storey, 1986). Anurans such as pelobatids and bufonids that can supercool but that are not freeze tolerant must find overwintering sites where temperatures do not fall below their supercooling limits and where ice is absent in order to survive overwintering (Swanson and Graves, 1995).

Typically, pelobatid and bufonid anurans avoid subfreezing temperatures by burrowing deeply in the soil during the winter (Breckenridge and Tester, 1961; Tester and Breckenridge, 1964; Ruibal et al., 1969; Swanson and Graves, 1995). Moreover, at least some species reposition themselves within their burrows to minimize exposure to subfreezing temperatures (Tester and Breckenridge, 1964; van Gelder et al., 1986). However, pelobatids and bufonids both burrow using specialized structures located on the hind feet (e.g., Brown et al., 1972). These 'spades' allow toads to burrow in friable and nonfriable soils. In contrast, *Pseudacris s. illinoensis* uses its front feet to burrow and is only able to construct burrows in friable soils (Brown et al., 1972).

Despite their difference in burrowing methods, *Pseudacris s. illinoensis* is similar to pelobatid and bufonid toads in the absence of freeze tolerance but differs from two of its congeners (*P. triseriata* and *P. crucifer*) both of which are freeze tolerant. Swanson and Graves (1995) noted that it is difficult to understand why toads depend on relatively energetically expensive burrowing to avoid subfreezing temperatures rather than development of mechanisms for freeze tolerance. They further noted that anuran cryoprotectant systems may also be energetically significant because they are carbohydrate based and some carbohydrate is lost during each freeze-thaw cycle (Storey and Storey, 1986; Swanson and Graves, 1995).

However, any explanation of evolution in overwintering strategies among pelobatid and bufonid toads is confounded by possible phylogenetic effects because no pelobatid or bufonid toad studied to date is freeze tolerant. The contrast between *Pseudacris s. illinoensis* that is not freeze tolerant and its two congeners that are freeze tolerant, thus, has important implications. In this instance, the absence of freeze tolerance in a burrowing species and the presence of freeze tolerance in terrestrial or arboreal species occurs within a single genus. This outcome is consistent with the hypothesis that cryoprotectant systems are energetically expensive and may be lost in fossorial species providing support for the conclusions of Swanson and Graves (1995). It is noteworthy that despite being a relatively specialized species of Hylidae (i.e., Brown et al., 1972; Paukstis and Brown, 1987 and 1991), *P. streckeri* is the only hylid from temperate North America that has not been found to be freeze tolerant (previous studies reviewed in Swanson and Graves, 1995).

However, all of the hylids previously studied have been from areas of North America where winter temperatures commonly reach low subfreezing temperatures (i.e., Swanson and Graves, 1995). No studies have been conducted of populations or species from the milder climates of the southern United States. It is also not known whether freeze tolerance and supercooling limits vary geographically in any anuran species. Studies of the painted turtle (*Chrysemys picta*) suggest that physiological responses to subfreezing temperatures may vary geographically (Packard and Janzen, 1996). If anuran cryoprotectant systems are energetically expensive, then they should be lost in populations that do not normally experience subfreezing temperatures overwinter.

Both *Pseudacris streckeri* and another closely related species, *P. ornata*, are distributed mainly in the southern United States (Conant and Collins, 1991) and both are fossorial (Brown et al., 1972; Brown and Means, 1984). Thus, the absence of freeze tolerance could be an adaptation to their fossorial habits (see above) or reflect their distribution in areas where freeze tolerance is not necessary for successful overwintering. Regardless, the absence of freeze tolerance in northern populations (i.e., *P. s. illinoensis*) may explain their restriction to habitats where they can burrow deeply to avoid subfreezing temperatures. Because their forward burrowing behavior is only efficient in sandy substrates, northern populations were only able to remain in areas of sandy substrates following the end of the post-Wisconsinan xerothermal period. Thus, we suggest that the current distribution of *P. s. illinoensis* is a function of their physiological responses to subfreezing temperatures.

Our field study indicates that to have survived the winter of 1996/1997 which was only moderately severe that frogs would have had to have burrowed to a depth of more than 12.5 cm. Such depths are commonly reached and exceeded by pelobatid and bufonid toads (e.g., Tester and Breckenridge, 1964; Swanson and Graves, 1995). Unfortunately relatively little is known of burrowing depths for *P. s. illinoensis* but previously discovered burrows are shallow (Axtell and Haskell, 1977; Tucker et al., 1995).

The actual depth that *P. s. illinoensis* burrows in winter is not known. Nonetheless unusually severe winters may affect this frog. For instance, the winter of 1995/1996 was unusually severe with one week long period during February where temperatures remained below -15°C. Moreover, snow cover was absent during this period. Although we observed no direct evidence of mortality, 67% of the specimens caught in the spring of 1996 had what appeared to be frost injuries (Fig. 9). These injuries were similar for the 20 frogs observed in that all were areas of discolored skin located on the dorsal side of the frog above the illial prominences. Most frogs also had discrete discolored areas at the ankles and knees (Fig. 9). Such injuries were not observed following the two preceding nor one following winter at the Sand Road site.

We suggest that these injuries occurred when the sand froze to a depth deep enough to include the roofs of burrows containing overwintering frogs. In each case injuries occurred to portions of the frog most likely to be in contact with the roof of the burrow. The natural occurrence of such injuries following a particularly severe winter indicates the importance of substrates that allow deep burrowing by *P. s. illinoensis* in northern regions.

Figure 9. Possible frost injuries to Illinois chorus frogs, *Pseudacris streckeri illinoensis.*

Figure 9

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